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New genus of Ignotalidae (Cicadomorpha) with notes on other Homoptera from the Permian and Triassic of the Tunguska Basin

Новый род Ignotalidae (Cicadomorpha) с замечаниями о других Homoptera из перми и триаса Тунгусского бассейна

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КЛЮЧЕВЫЕ СЛОВА: Hemiptera, Auchenorrhyncha, Pereborioidea, эволюция, биогеография, пермотриасовый кризис.

ABSTRACT. *Ilimpeika humerosa* **gen.** et **sp.n.** from the Upper Permian of the Tunguska Basin is the first representative of the family Ignotalidae (known from South Africa and South China) in the northern extratropical zone. *Megoniella* Riek, 1973 = *Perissovena* Riek, 1976, **syn.n.**; *M. multinerva* Riek, 1973 = *P. heidiae* Riek, 1976, **syn.n.** Brief notes are given on other finds of Homoptera in the Permian and Triassic of the Tunguska Basin.

РЕЗЮМЕ. *Ilimpeika humerosa* **gen.** et **sp.n.** из верхней перми Тунгусского бассейна – первый представитель семейства Ignotalidae (известного из ЮАР и Южного Китая) в северной внетропической зоне. *Megoniella* Riek, 1973 = *Perissovena* Riek, 1976, **syn.n.**; *M. multinerva* Riek, 1973 = *P. heidiae* Riek, 1976, **syn.n.** Кратко охарактеризованы семейства равнокрылых, отмеченные в перми и триасе Тунгусского бассейна.

The large polyneurous cicada wings from the Upper Permian of South Africa, separated into the family Ignotalidae and the superfamily Ignotaloidea, were considered to support the view that Homoptera descended from Protoblattodea [Riek, 1973]. Later, this family was included in Pereborioidea, and three genera from the Upper Permian of China [Lin, 1982] were added [Shcherbakov, 1984, 2000]. The Triassic genus *Beaconiella* Evans, 1963, included in Ignotalidae by Riek [1973], was transferred to another pereborioid family, Curvicubitidae [Shcherbakov, 1996, 2021]. Extreme polymerization of veins in some pereborioids was accompanied by the loss of such basic features of the Hemiptera forewing as the fusion of Sc with R (except for the base and apex) and distal fusion of claval veins [Shcherbakov, 2021]. However, the earliest members of the superfamily (such as Middle Permian *Scytophara* Martynov, 1937; Pereboriidae) confirm that the group originated from typical early Cicadomorpha, namely from Prosbolopseidae [Shcherbakov, 1984].

In the second half of the 20th century, geological and paleontological parties collected a significant number of fossil insects from the Permian and Triassic of the Tunguska Basin in Central Siberia, but only a small part of this material has been described. A new genus of Ignotalidae from the Upper Permian of the Tunguska Basin is established below, and brief notes are given on other Homoptera families known from these strata.

The material is deposited at the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken with a Nikon D70 digital camera. The vein nomenclature is after Shcherbakov [1984, 1996].

Superfamily Pereborioidea M.Zalessky, 1930
Family Ignotalidae Riek, 1973

REVISED DIAGNOSIS. Moderately to very large, extremely polyneurous cicadas. Tegmen: Costal margin strongly convex at least proximally, area anterior to Sc wide. Sc free or distally connected with RA, with weak prenodal branches. Basal cell reduced. Membrane without punctures or granules. Hind wing: Costal margin strongly convex at base, nearly straight distally, with series of coupling hooks. R stem short and oblique; R with several, M with few, and CuA with many branches in bundle.

COMPOSITION. *Ignotala* Riek, 1973; *Megoniella* Riek, 1973 (= *Perissovena* Riek, 1976, **syn.n.**); *Rhipiscytina* Lin, 1982; *Furcascytina* Lin, 1982; *Scopiprosbole* Lin, 1982; *Ilimpeika* Shcherbakov, **gen.n.**

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REMARKS. *Perissovena heidiae* Riek, 1976, based on a hind wing from the Upper Permian of South Africa, has been assigned with some reservations to the family Pereboriidae (known from Russia and Brazil) with a note that it could possibly be the hind wing of *Megoniella multinerva* Riek, 1973 [Riek, 1976]. This hind wing is similar to that of *Ilimpeika* **gen.n.**, so the synonymy suggested by E.F. Riek is confirmed: *Megoniella multinerva* Riek, 1973 (= *Perissovena heidiae* Riek, 1976, **syn.n.**).

Ilimpeika Shcherbakov, **gen.n.**

TYPE SPECIES. *I. humerosa* Shcherbakov, **sp.n.**

DIAGNOSIS. Large cicadas. Tegmen: Costal margin arched over most of its length. Broad area anterior to Sc with very low ridge along midline (C and its continuation) separating precostal and costal areas of subequal width. Sc free, not fused with R medially, prenodal branches sparse. M forked distal to R, forming short stalk with CuA near base; CuA stem convex. RP and MA forked more basally than CuA. Veins in prenodal part much less distinct and close-set than subparallel branches connected with strong crossveins in postnodal part. Hind wing: RP and M forked about wing midlength.

COMPOSITION. Type species.

COMPARISON. Similar to the monotypic Late Permian *Ignotala* Riek, 1973 from Natal in the large size, the wide precostal area separated by a low ridge, and close-set up-arched veins with distinct crossveins in the postnodal part of the tegmen, but the latter genus has the tegmen twice larger with Sc and R connected distally, M forked before R and not forming a short stalk with CuA, and the hind wing with M forked more distally.

ETYMOLOGY. From Ilimpeya River (type locality); gender feminine.

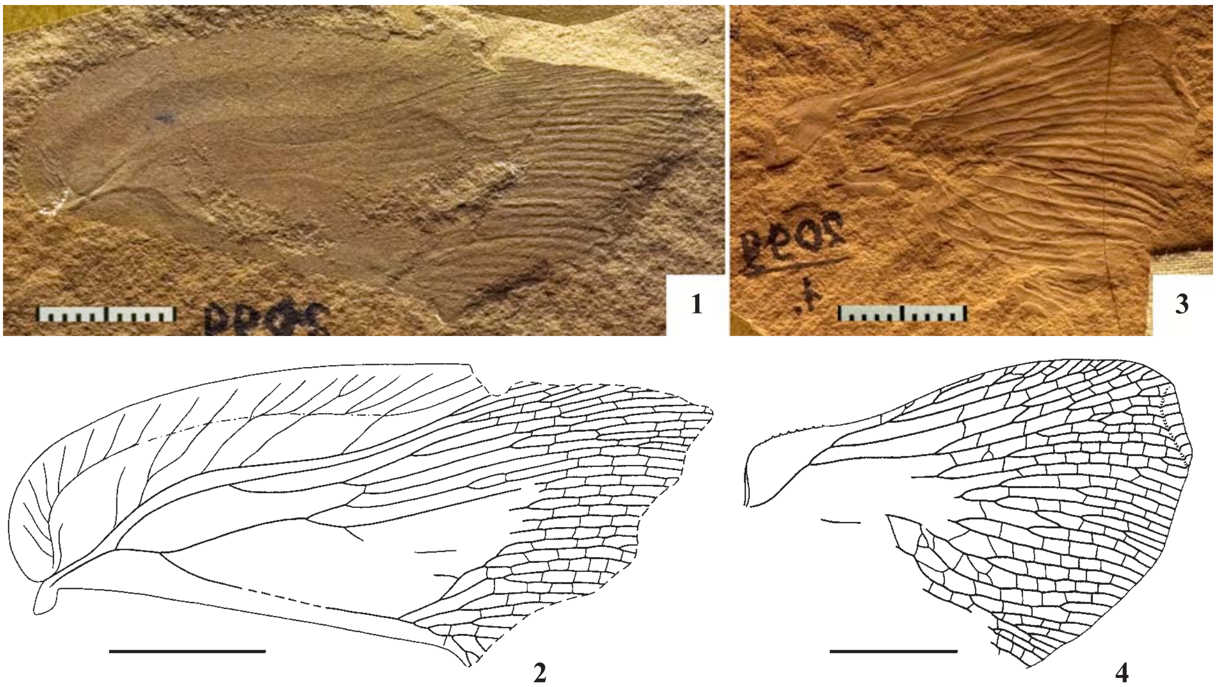
Ilimpeika humerosa Shcherbakov, **sp.n.**
Figs 1–4

MATERIAL. Holotype PIN 2099/2, incomplete right tegmen (clavus missing) on reddish burnt carbonaceous siltstone; paratype PIN 2099/1, left hind wing (anal area missing) on orange burnt siltstone; Krasnoyarsk Krai, Evenkiysky District, right bank of the Ilimpeya River 3.3 km downstream of the Ukshun(n)ukan River, collected by N.I. Emelyanov (All-Union Aerogeological Trust) in 1962; locality Ilimpeya, or Red Cliff (Красный утёс) [Meyen, 1966], or Ukshunukan-2 (outcrop 716 of G.N. Sadovnikov); 62.25°N, 105.29°E; Degali Formation [Meyen, 1966], Upper Permian.

DESCRIPTION. Tegmen 47 mm long and 19 mm wide as preserved (estimated full length ca. 60 mm), elongate. Prenodal Sc branches weak, not branched profusely and not turned longitudinal towards wing margin. RA apparently with at least 4 branches, RP with about 6, M and CuA with about 10 branches each. Distinct crossveins only in postnodal part (except for one nodal *r-m*), numerous, slightly inclined distally, more close-set in CuA area. Hind wing 35 mm long and 22 mm wide as preserved, much shorter than tegmen. Costal margin strongly arched at base, with about ten strong coupling hooks. R stem short and oblique, RA with 3 main branches, RP with 6 branches, M with 3 or 4, CuA with bundle of at least 13 branches. Colour pattern on wings not preserved.

REMARKS. The locality was listed among those with the Korvunchana flora of possible Early Triassic age (and the formation was mentioned as the Limptekon Formation) [Shcherbakov, 2000; Ponomarenko, Shcherbakov, 2004; Ponomarenko, 2006], but in fact it is rich in cordaites, belongs to the Degali Formation s.str. (lower subformation of the former Degali Formation s.l.) and is undoubtedly Late Permian [Meyen, 1966].

ETYMOLOGY. From Latin *humerus* (shoulder).



Figs 1–4. *Ilimpeika humerosa* **gen.** et **sp.n.**: 1–2 — holotype tegmen: 1 — photograph (mirrored); 2 — venation (dash-dotted, boundary of precostal area); 3–4 — paratype hind wing: 3 — photograph (mirrored); 4 — venation. Scale bars: 10 mm.

Рис. 1–4. *Ilimpeika humerosa* **gen.** et **sp.n.**: 1–2 — голотип, переднее крыло: 1 — фото (отражено зеркально); 2 — жилкование (штрих-пунктиром граница прекостального поля); 3–4 — паратип, заднее крыло: 3 — фото (отражено зеркально); 4 — жилкование. Масштаб: 10 мм.

Discussion

In the Tunguska Basin, Homoptera fossils have been recorded from coal-bearing deposits with cordaite flora and from intertrappean beds with the so-called Korvunchana flora. In the Upper (and possibly uppermost Middle) Permian of the Pelyatka and Degali Formations, the families Prosbolidae (Prosboloidea), Pereboriidae and Ignotalidae (Pereborioidea), Stenoviciidae and Paraknightiidae (Scytinopteroidea) are found. It is noteworthy that no Homoptera have been recorded in the older deposits of the Tunguska Basin. Scytinopteroids, which presumably lived on helophytes and other waterside vegetation, numerically dominate in some localities, e.g. the insect assemblage of the Kerbo-1 locality (Gagariy Ostrov Formation) almost entirely consists of numerous nymphs and few adults of one Paraknightiidae species [Shcherbakov, 2000].

Intertrappean beds with the floras rich in lycopods or conifers and ferns are usually considered Lower Triassic (see Mogucheva [2016]), although there is increasing evidence that at least the lower of these formations lie below the Permian–Triassic boundary (PTB) of the International Stratigraphic Scale. Insect fossils have been found in intertrappean beds of the Bugarikta, Nidym and Kochechumo Formations, which are all Lower Triassic after the regional stratigraphic scheme [Saks et al., 1981] or all Upper Permian after Sadovnikov [2015], but may turn out to be so-called "boundary beds" with the PTB between the Bugarikta and Nidym formations (see Shcherbakov et al. [2021]).

Moderately diverse Dysmorphoptilidae (Prosboloidea) are common in the Bugarikta Formation (localities Anakit and Khungtukun). One of these dysmorphoptilids is *Unturella truncata* Shcherbakov, 2022, described from several tegmina from the Khungtukun-2 and Untuun-2 localities, the latter locality being currently assigned to the Kochechumo Formation (Agitkan Sequence) [Shcherbakov, 2022], so this species probably crossed the PTB. The most basal homopterans, Archescytinidae (Paleorrhyncha), known since the Early Permian, are last recorded in the Bugarikta Formation (and the Permian–Triassic boundary beds of Nedubrovo, Vologda Region) [Shcherbakov, 2000]. Other Homoptera families recorded from the Bugarikta Formation are Surijokocixiidae (Fulgoroidea), Scytinopteridae and Stenoviciidae (Scytinopteroidea). Two species of Surijokocixiidae (*Boreocixius sibiricus* Becker-Migdisova, 1955, *B. rotundatus* Becker-Migdisova, 1955) were described from the beds correlated with the Bugarikta Formation in the buried part of Siberian Traps outside the Tunguska Basin (borehole at the left bank of Yenisey River near the mouth of Malaya Kheta River 150 km WNW of Norilsk) [Becker-Migdisova, 1955]. The third species of this genus was recently described from the Middle Triassic (Ladinian) of Tongchuan, China [Zhang et al., 2021].

The only Homoptera found in the Nidym Formation is *Rhipiscytina* sp. (Ignotalidae) from the Lake Severnoe [Shcherbakov, 2000, 2008]. The genus *Rhipiscytina* Lin, 1982, described from the Longtan Formation (Wuchiapingian, 259.1–254.14 Ma [Wang et al., 2022]) of South China (Jiangsu) at 32°N, was also recorded from the Permian–Triassic boundary beds (about 251.9 Ma) of the Putorana Plateau at 67°N, at a distance of 4200 km from the Chinese locality. *Rh. brimis* Lin, 1982 lived at 14°N paleolatitude (paleocoordinates from the Paleobiology Database [2022]) in the Late Permian tropics of Cathaysia, on the South China microcontinent amidst the warm ocean. The Late Permian Cathaysian flora of South China, which flourished in warm and humid conditions after the Emeishan Traps eruption, disappeared during the end-Permian mass extinction [Luo et al., 2021], but served as the main source of the Korvunchana flora [Dobruskina, 1994]. The *Rhipiscytina* species from the Tunguska Basin lived at 55°N paleolatitude in the Early Triassic semiarid zone (see Romano et al. [2020]), amidst the Pangaea supercontinent, at least a thousand km from any sea. This northward shift of the *Rhipiscytina* range by 40 degrees of latitude is consistent with the idea of a poleward shift of climatic zones due to catastrophic warming at the Permian–Triassic transition [Chumakov, Zharkov, 2003]. Analogous distribution shifts were reported in terrestrial tetrapods [Benton, 2018].

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